

LINKING SEEDLING SPATIAL PATTERNS TO SEED DISPERSAL PROCESSES IN AN INTERMITTENT STREAM

JOHN M. BOLAND

Southwest Wetlands Interpretive Association, 700 Seacoast Drive #108, Imperial Beach, CA 91932

JohnBoland@sbcglobal.net

ABSTRACT

To better understand the colonization of bare riparian sites, I examined seedling distribution patterns and seed dispersal processes of 11 common riparian species. The study site was two in-channel sedimentation basins on an intermittent stream flowing into the Tijuana River Valley, southern California. The 11 species relied on one of two vectors to disperse seeds into the basins, either water or wind. Seven species dispersed to the basins via winter stream flows and, of these, three grew mainly at the basin periphery and four grew mainly in the bed. Seed buoyancy tests and tests of dispersal using seed mimics showed that, for these species, the main process producing seedling distributions was that of sorting of the seeds by the stream flows based on seed buoyancy. Most past work on seed dispersal in riparian habitats has been conducted in perennial systems where non-buoyant seeds usually remain in deep water and never germinate, and this has led to the notion that non-buoyant seeds are not effectively dispersed by water. This study shows that non-buoyant seeds are effectively dispersed by flows in intermittent systems because the seeds were able to germinate and grow once the bed had dried. Four species dispersed to the basins via wind, and their seedlings grew in concentric bands around the basins. Monitoring of seed production and tracking of the basin's water level showed that, for these species, seedling distributions were the result of staggered periods of seed dispersal and gradual decline of the water level. Only three of these 11 species were abundant in the five- and 22-year old stands examined, i.e., the wind-dispersed *Baccharis salicifolia* (Ruiz & Pav.) Pers., *Salix lasiolepis* Benth., and *S. gooddingii* C.R. Ball. A banding pattern established at the time of recruitment, with *S. lasiolepis* higher on the bank than *S. gooddingii*, was retained in the older forests, making this one of very few examples that show a direct link between seed dispersal processes, seedling distributions, and adult distributions. This study provides insight into the early development of riparian woodlands by identifying and explaining distribution patterns in water- and wind-dispersed colonizers.

Key Words: anemochory, hydrochory, natural restoration, pleustochory, seed buoyancy.

Within river corridors, bare areas of riverbank can be quickly colonized by a suite of riparian plants that arrive from elsewhere. Rapid colonization is a common phenomenon, yet the seed dispersal processes that underlie seedling establishment are not well understood (Briggs 1996; Gurnell et al. 2006). Because the spatial distribution of the colonizers may persist for decades as a forest matures, understanding colonization is of enormous value (Willson and Traveset 2000; Boland 2014a).

Riparian plants rely on two main vectors to disperse their seeds and other propagules—flowing water and wind. Dispersal via flowing water, termed hydrochory, has been shown to be important in the transport of riparian plant seeds (Tabacchi et al. 2005) and establishment of riparian species in disturbed areas (Gurnell et al. 2006, 2008). Seed buoyancy is considered essential for water-dispersal, as most of the seeds entering riparian corridors are deposited along bankfull drift lines with other buoyant debris, particularly after seasonal floods (Vogt et al. 2006, 2007). Emphasis in the study of water-dispersal has been on long-distance dispersal along rivers (Johansson et al. 1996), but the influence that water-dispersed seeds have on riparian vegetation community composition and structure is still

being debated (Danvind and Nilsson 1997; Andersson et al. 2000; Levine and Murrel 2003; Jansson et al. 2005; Nilsson et al. 2010).

Seed dispersal via wind, termed anemochory, is typical of many riparian trees, such as willows (*Salix* L. spp.) and cottonwoods (*Populus* L. spp.). Seeds of wind-dispersed plants are usually small and have hairs or outgrowths that increase their surface area to catch the wind (Matlack 1987; Karrenberg et al. 2002). The seed shadow of wind-dispersed plants typically peaks near the parent plant and declines rapidly with distance outwards (Willson 1983; Bullock and Clarke 2000), and most studies of wind-dispersal, like those of water-dispersal, have focused on long-distance dispersal (Nathan and Muller-Landau 2000; Nathan et al. 2002). Unlike water-dispersal, wind-dispersal has been shown to be a key factor in structuring some riparian woodlands in southern California (Boland 2014a).

Here I examine the colonization of large bare areas to better understand the processes that produce spatial patterns in a young riparian community. The bare areas were within two sedimentation basins that were cleaned out each fall and so allowed observation of a new crop of recruited seedlings each year. Initial observations showed that some colonizing

species arrived via water-dispersal during winter flows and others arrived via wind-dispersal during spring. My general approach in this study was to describe the patterns in the distribution of recruiting seedlings and to link these patterns to the underlying processes that produced them. In particular, I addressed the following questions:

1. Among the water-dispersed species, what is the distribution of seedlings within the basins, and can the distributions be attributed to the buoyancy characteristics of their seeds?
2. Among the wind-dispersed species, what is the distribution of seedlings within the basins, and can the distributions be attributed to the timing of their seed dispersal?
3. What roles do the colonizing species play in the structure of older riparian woodlands and forests?

This study of the distribution of riparian seedlings is one of very few that examines water-dispersal and wind-dispersal simultaneously and is the first to do so in an intermittent stream.

METHODS

Study Site

This research was conducted from 2012–2015 at the Goat Canyon sedimentation basins in Border Field State Park, Tijuana River Valley, San Diego County, California (32°32.459'N, 117°6.374'W). The two earthen, in-channel basins constituted a 520 m reach of an intermittent stream that drains a small, coastal watershed (<20 km²). The basins, which together hold approximately 45,000 m³ of sediment, were cleaned out each year in fall (September and October). The clean-out removed all plants, seeds, and debris, along with the accumulated sediment. River flows then refilled the basins with water and sediment during the rainy season (November to March). Deposited sediment was composed of mostly fine sand and silt (Boland 2014b). After the rainy season, the basins contained large, shallow pools (13,000 to 15,000 m²) that slowly drained and evaporated during spring and summer and eventually dried completely by the end of summer (Fig. 1). Apart from the sediment removal in fall, the basins were left undisturbed and seedlings were allowed to establish naturally and, thus, the basins provided a suitable site at which to examine seed dispersal and patterns of seedling recruitment.

Plant Species

This research focused on 11 plant species that recruited abundantly in the basins and in disturbed riparian sites elsewhere in the valley. These included species that were water- and wind-dispersed, native and non-native, annual and perennial, and forbs, shrubs and trees (Table 1). For ten of these, the dispersing propagule was a single seed, and for one (*Xanthium strumarium* L.) it was a bur containing

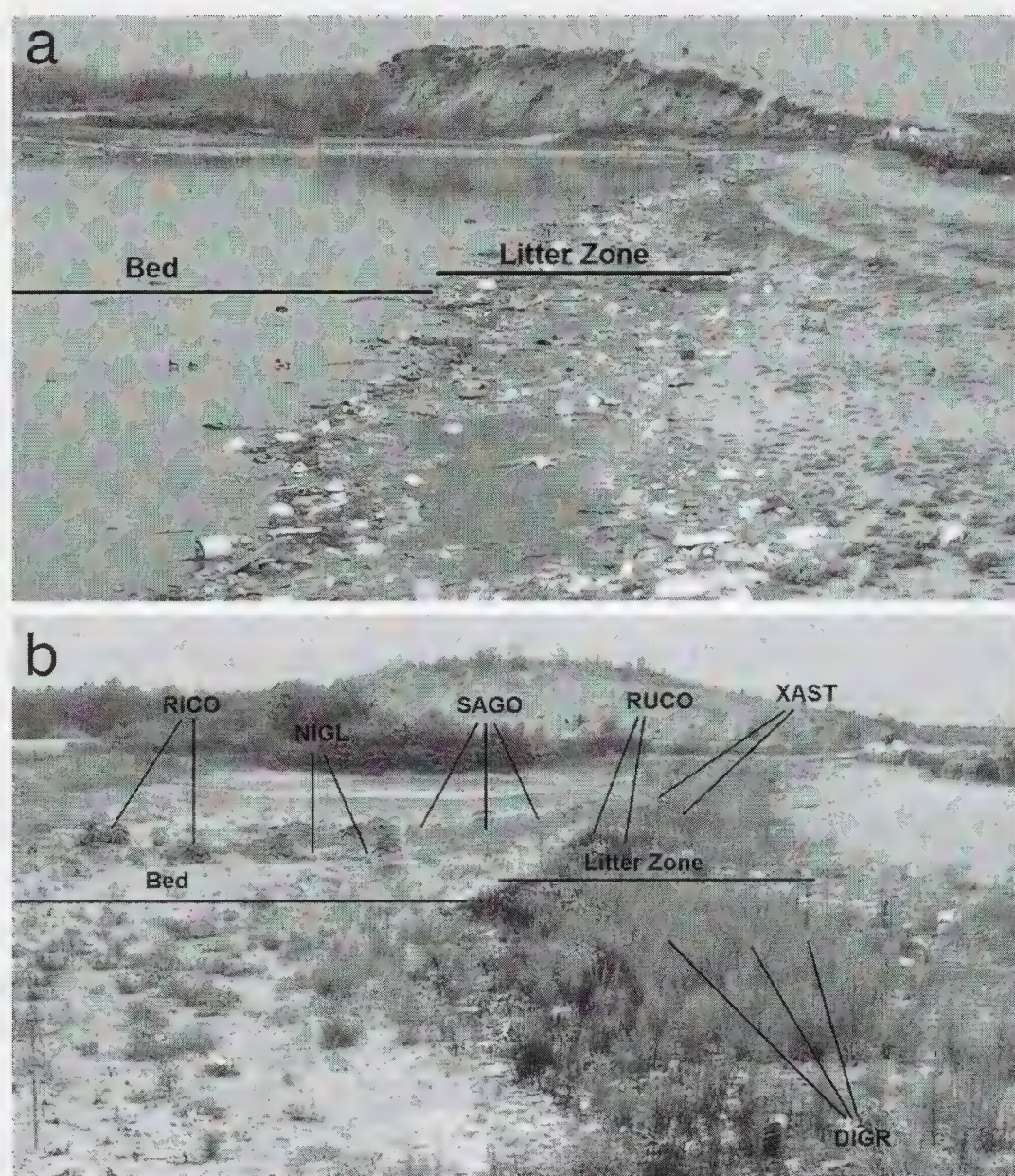


FIG. 1. The lower Goat Canyon sedimentation basin during March (above) and September (below). In March, the water level is a little below the bankfull maximum; the Litter Zone is exposed and the Bed is underwater. In September, the pool has dried exposing both the Litter Zone and the Bed. The Litter Zone is densely vegetated with several species, including the water-dispersed *Rumex conglomeratus* (RUCO) and *Xanthium strumarium* (XAST) and the Bed is sparsely vegetated with several species, including the water-dispersed *Ricinus communis* (RICO) and *Nicotiana glauca* (NIGL). The wind-dispersed species are present in bands; two are indicated—*Dittrichia graveolens* (DIGR) and *Salix gooddingii* (SAGO).

two seeds; for convenience, the term ‘seed’ was used in this paper for all 11 species.

Seedling Pattern #1—Water-Dispersed Species

a) *Seedling distribution.* To document the seedling distribution pattern of the seven water-dispersed species, the basin area that was underwater during the winter floods was divided into two zones: the Litter Zone and the Bed (Fig. 1). The Litter Zone, so named because it contained abundant buoyant trash, was the high zone around the basin periphery near bankfull stage. In summer 2014, this zone was 6–29 m wide and had a total area of 8,446 m². The Bed was the rest of the basin down-slope from the Litter Zone. It contained little or no buoyant trash. In summer 2014, the Bed was 36–60 m wide and had a total area of 19,963 m². Fifteen stratified-random transects (20 m long) were placed in each zone during August and September 2014. Along each transect, seedlings of the water-dispersed species were counted within ten quadrats (75 × 75 cm) placed at two-meter intervals, for a total of 150 quadrats per zone (i.e., 10

TABLE 1. Characteristics of the common species in the Goat Canyon sedimentation basins. Origin is native (N) or non-native (X); growth form is forb (F), shrub (S) or tree (T); life span is annual (A) or perennial (P); seed length measurement is for the seed alone and, where applicable, for the seed plus the length of the seed’s attached hairs or pappus (given in parentheses). The cocklebur seed length is for the bur. All details are from Jepson Manual (Baldwin 2012), except ‘a’ which are from Lightner (2011) and ‘b’ which are from Boland (unpublished; n = 10–20 dispersing seeds).

Species	Dispersal method	Common name	Origin	Growth	Life span	Seed length (mm)
<i>Rumex conglomeratus</i> Murray	Water	Whorled dock ^a	X	F	P	1.5–2.0
<i>Xanthium strumarium</i> L.	Water	Cocklebur	N	F	A	10–30+
<i>Persicaria lapathifolia</i> (L.)	Water	Willow weed	N	F	A	1.5–3.2
<i>Ricinus communis</i> L.	Water	Castor bean	X	S	P	9–22
<i>Nicotiana glauca</i> Graham	Water	Tree tobacco	X	S	P	0.5–0.7 ^b
<i>Solanum americanum</i> Mill.	Water	White nightshade ^a	N	F	P	1.0–1.5
<i>Datura wrightii</i> Regel	Water	Jimson weed	N	F	P	5.0
<i>Dittrichia graveolens</i> (L.)	Wind	Stinkwort	X	F	A	2.0 (3–5)
<i>Salix lasiolepis</i> Benth.	Wind	Arroyo willow	N	T	P	0.8–1.2 (10–15) ^b
<i>Baccharis salicifolia</i> (Ruiz & Pav.) Pers.	Wind	Mule fat	N	S	P	0.8–1.3 (3–6)
<i>Salix gooddingii</i> C.R. Ball	Wind	Goodding’s black willow	N	T	P	0.8–1.2 (10–15) ^b

quads × 15 transects). For each species, abundance in the two zones was tested against the expected values of 50% in each zone using the G-test for goodness-of-fit (Sokal and Rohlf 1995).

I developed a simple index called the Litter Zone Percentage to describe the overall distribution of each species. The index indicated a species’ relative abundance in the Litter Zone and was calculated in the following manner:

$$\text{Litter Zone Percentage}_X = (D_L \cdot A_L)(100)/(D_L \cdot A_L + (D_B \cdot A_B))$$

where D_L is the average density of species x in the Litter Zone, A_L is the total area of the Litter Zone, D_B is the average density of species x in the Bed, and A_B is the total area of the Bed. A species with a Litter Zone Percentage of more than 50% had most of its seedlings in the Litter Zone, whereas a species with a Litter Zone Percentage of less than 50% had most of its seedlings in the Bed.

b) *Seed buoyancy.* To measure the floating ability of seeds of the water-dispersed species, ripe seeds were collected in the Goat Canyon area in November 2014, prior to the first winter rains. The seeds were stored dry at room temperature, and their buoyancy was tested three times in the lab during the following December and January. Each trial started on the first day of a rainstorm when the seeds likely would have been dispersed by stream flows. In each trial, 50 seeds of each species were placed in empty seven-oz plastic cups, ten seeds per cup, except for *X. strumarium*, which had one bur per cup. Approximately 125 ml of water was then poured into each cup and the number of floating seeds was counted at the following times: 0.1, 0.5, 1, 2.5, 4, 6.5, 12, 24, 36, 48, and 72 hr after initial immersion. Before each count, the seeds in each cup were sprayed with water from a mister to dislodge any that were floating because of surface tension alone. Other researchers have stirred seeds for the

same reason (e.g., Danvind and Nilsson 1997) but I found that stirred seeds adhered to the stirrer and sides of the cup so spraying was more effective. Seed buoyancy was calculated for each species as the average length of time seeds floated, with a maximum of 72 hr. The strength of the link between seed buoyancy and seedling distribution (Litter Zone Percentage) was quantified using correlation analysis (Sokal and Rohlf 1995).

c) *Dispersal of seed mimics.* To test whether buoyant seeds accumulated in the Litter Zone and non-buoyant seeds accumulated in the Bed, I released buoyant and non-buoyant seed mimics upstream of the basins. Buoyant seed mimics were ping-pong balls (Momentum Brands by Dollar Empire LLC, Vernon, CA; recreational grade; 40 mm diameter; weight = 2.7 g) and non-buoyant seed mimics were ping-pong balls filled with sand (mean weight = 42.4 ± 3.8 g). Non-buoyant balls were prepared by drilling a hole in the ball, inserting the end of a streamer, filling the ball with sand, and sealing the hole with hot glue. The streamer, added to aid in the detection of buried balls, was made of polypropylene curling ribbon (0.5 cm wide and 75 cm long). Just before a rainstorm, I placed fifty balls of each type together in the dry streambed, approximately 50 m upstream of the basins. This was done on two occasions: 22 April 2015 and 8 May 2015. The balls were washed downstream with the subsequent storm flows and over the next few weeks, as the pools dried, I searched for the balls. The location of each ball was mapped using a handheld GPS unit (Garmin eTrex Venture HC) and determined to be in the Litter Zone or the Bed of the basin, based on the positions of the zone of stranded buoyant trash and the thalweg. Abundances of the buoyant and non-buoyant seed mimics in the two zones were compared using the G-test of independence (Sokal and Rohlf 1995).

Seedling Pattern #2—Wind-Dispersed Species

a) Seedling distribution and water level. To describe the seedling distribution pattern of the four wind-dispersed species, I used methods similar to those used in a prior study (Boland 2014b) and suited to the high seedling densities and narrowly banded distributions. I first monitored the decline of the water's edge and then surveyed the seedlings along that timeline. During winter 2014, a vertical transect was started at a randomly-chosen site around the lower basin, and the water's edge was marked with wooden stakes every 3–4 wk from 13 December 2014 to 20 July 2015. The stakes established a timeline of the lowering water level and the associated moist fringe of sediment around the pool. In August 2015, a vertical transect (15 m) was placed next to the timeline transect, from the highest to the lowest water levels, and seedlings of the wind-dispersed species were counted within quadrats (20×20 cm) placed end-to-end along the transect for a total of 75 quadrats.

b) Timing of seed production by adults. Seed production of the four wind-dispersing species was monitored to determine their periods of seed dispersal. In *Dittrichia graveolens*, the percent cover of fruiting flower heads was recorded every 3–12 d for the same 15 adult plants in Goat Canyon from 11 December 2014 to 12 January 2015. In the other three species, adult female plants were monitored weekly from 5 February 2013 through 25 June 2013. Each week the same individuals of *Salix lasiolepis* ($n = 12$), *Salix gooddingii* ($n = 15$), and *Baccharis salicifolia* ($n = 12$) were visited in the Tijuana River Valley, and the percent cover of fruiting catkins (or flower heads in the case of *B. salicifolia*) was estimated following the procedure described in Boland (2014a). A mean percent cover was calculated for each species on each monitoring date. All percent cover estimates were of mature, fluffy seeds that were ready to disperse. The strength of the link between the species' seedling distributions and timing of seed dispersal was quantified using correlation analysis (Sokal and Rohlf 1995).

Community Development

To describe the early successional changes that occur after recruitment and the roles played by the 11 species in developing riparian woodlands, I conducted surveys at three Tijuana River Valley sites with woodland stands of different ages. Surveys were conducted in summer 2015, and the stand ages were 0.5 yr (Goat Canyon lower basin), 5 yr (Site B at Dirt Road), and 22 yr (Site 1 at Bisect). The latter two are young forests described in Boland (2014a). At each site, the riparian habitat was divided into three strata based on elevation—High (floodplain), Intermediate (bankfull stage), and Low (bed)—and a 25-m transect was randomly placed in

each stratum perpendicular to the slope. Along each transect, the percent cover of each of the 11 species was determined using the line-intercept method, and an additional 250 m² was searched to mark as present or absent any of the 11 species not found along the transect. Also, along each transect at the 0, 12.5, and 25 m positions, maximum canopy height was measured with a meter stick, stiff meter tape, or laser distance measurer (Bosch DLR130K) and percent canopy cover measurements were taken 1.15 m above ground level using a spherical densiometer (Forest Densiometers).

RESULTS

Seedling Pattern #1—Water-Dispersed Species

a) Seedling distribution. The water-dispersed species had many seedlings in the basins during summer, with densities up to 7.91 seedlings per m² (Table 2). Seedlings of all seven species were significantly more abundant in one or the other of the two zones (G-test for goodness-of-fit; $P < .01$). *Rumex conglomeratus* Murray, *X. strumarium* and *Persicaria lapathifolia* (L.) Gray were significantly more abundant in the Litter Zone and had Litter Zone Percentages of 85% or greater. In contrast, *Ricinus communis* L., *Nicotiana glauca* Graham, *Solanum americanum* Mill., and *Datura wrightii* Regel were significantly more abundant in the Bed and had Litter Zone Percentages of 10% or less.

b) Seed buoyancy. The seven species fell into two groups: *R. conglomeratus*, *X. strumarium*, and *P. lapathifolia* had buoyant seeds with average floating times of 23.5 hours or longer; whereas *R. communis*, *N. glauca*, *S. americanum*, and *D. wrightii* had sinking seeds with average floating times of 5.1 hr or less (Table 2). Seedling distribution (Litter Zone Percentage) was significantly correlated with seed buoyancy ($r^2 = 0.755$; $n = 7$; $P < 0.05$) indicating that species with buoyant seeds grew mainly in the Litter Zone, whereas species with sinking seeds grew mainly in the Bed.

c) Dispersal of seed mimics. Ninety-five of the 100 buoyant balls released were recovered, and 96 of the 100 non-buoyant balls released were recovered, a recovery rate of 95% and 96%, respectively. The buoyant and non-buoyant balls accumulated in different areas of the basins. Most of the buoyant balls (93 of 95, or 98%) were found in the Litter Zone and all of the non-buoyant balls (96 of 96, or 100%) were found in the stream thalweg and Bed. The distributions of buoyant and non-buoyant balls were significantly different (G-test of independence: $G = 245$, $P < .001$), indicating that differences in buoyancy could account for their dispersal into different zones. These results strongly suggest that seedling distributions of the seven water-dispersed

TABLE 2. Seedling densities and seed buoyancies of water-dispersed species. Seedling densities are the average number of individuals per m² in the two zones—Litter and Bed (n = 150 quadrats per zone). Seed buoyancy is the average number of hours afloat (n = three trials; 72 hr maximum). The G statistic is for the g-test for goodness-of-fit (an * indicates the test was done using the Yates continuity correction); Std d. = standard deviation; n = number of seedlings counted.

Species	Density						Litter zone percentage	Buoyancy		
	Litter zone		Bed zone		n	G statistic		P	Avg	Std d.
	Avg	Std d.	Avg	Std d.						
<i>Rumex conglomeratus</i>	7.91	11.32	0.00	0.00	667	924	<0.001	100%	71.6	0.6
<i>Xanthium strumarium</i>	4.05	6.47	0.21	0.77	360	356	<0.001	89%	23.5	4.9
<i>Persicaria lapathifolia</i>	0.46	1.64	0.04	0.25	42	36.6	<0.001	85%	34.3	7.4
<i>Ricinus communis</i>	0.28	1.11	1.03	2.40	111	37.9	<0.001	10%	5.1	0.3
<i>Nicotiana glauca</i>	0.19	1.01	1.16	2.14	114	65.5	<0.001	6%	4.3	2.3
<i>Solanum americanum</i>	0.01	0.15	0.84	1.66	72	89.2	<0.001	1%	0.1	0.0
<i>Datura wrightii</i>	0.00	0.00	0.12	0.57	10	9.9*	<0.01	0%	3.9	1.1
Total	12.91		3.40							

species can be attributed to the buoyancy characteristics of their seeds.

Seedling Pattern #2—Wind-Dispersed Species

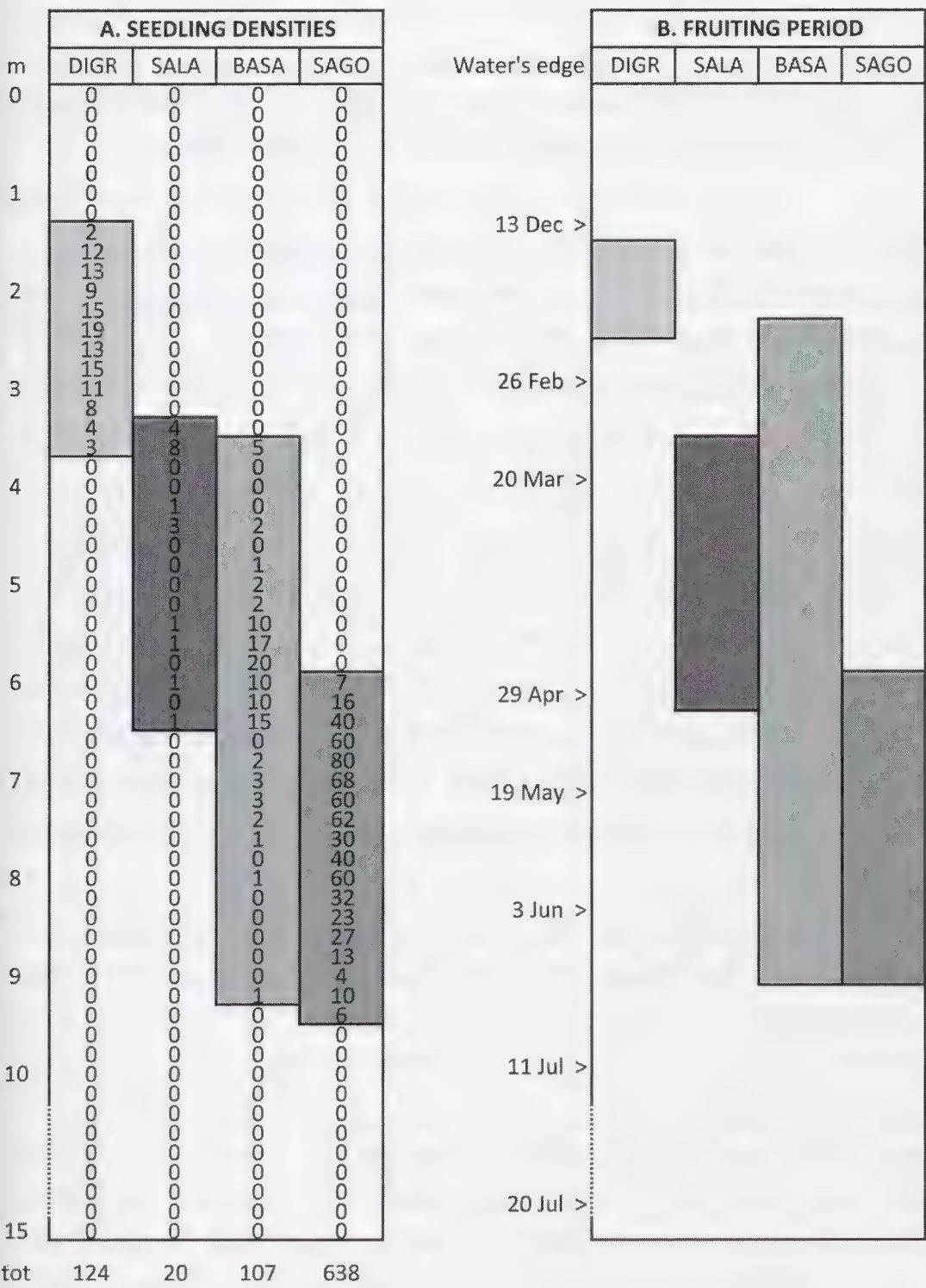


FIG. 2. Seedling densities and fruiting periods of the wind-dispersed species along the vertical transect. Seedling densities are the number of seedlings per quadrat (400 cm²); the distribution of each species is enclosed in a shaded box. Fruiting periods are from Fig. 3, displayed on the vertical transect according to the position of the water's edge on given dates; the fruiting period of each species is enclosed in a shaded box. DIGR = *D. graveolens*, SALA = *S. lasiolepis*, BASA = *B. salicifolia* and SAGO = *S. gooddingii*.

a) *Seedling distribution and water level.* The four wind-dispersed species had abundant seedlings in the basins during summer with densities up to 80 seedlings per quadrat (Fig. 2A), or 2,000 seedlings per square meter. Seedlings of three of the species were distributed at relatively distinct levels along the transect and grew in concentric bands around the basin; *Dittrichia graveolens* (L.) Greuter formed the highest band, *S. lasiolepis* the middle band, and *S. gooddingii* the lowest band. *Baccharis salicifolia* seedlings were distributed more widely and overlapped with those of *S. lasiolepis* and *S. gooddingii*. The water level in the basin was highest on 13 December 2014 and declined gradually during spring and summer 2015 until August, when the entire transect line site was dry (Fig. 2). The moist fringe at the water's edge, so important for recruitment, moved gradually down the transect with the declining water level.

b) *Timing of seed production by adults.* The four wind-dispersed species had different periods of seed production (Fig. 3). The seeds of three species were ripe and ready for dispersal during relatively short, discrete periods: *D. graveolens* dispersed first with a peak in December, *S. lasiolepis* dispersed next with a peak in early April, and *S. gooddingii* dispersed later with a peak in late May. *Baccharis salicifolia* dispersed seeds over a longer period that overlapped *S. lasiolepis* and *S. gooddingii*. When the timing of seed production was displayed on the timeline for the position of the water's edge (Fig. 2B), the seed production pattern largely matched the seedling distribution pattern of the four species (Fig. 2A). In both seedling densities and fruiting period, *D. graveolens* formed the highest band, *S. lasiolepis* the middle band, *S. gooddingii* the lowest band and *B. salicifolia* was widely overlapping. Along this time-

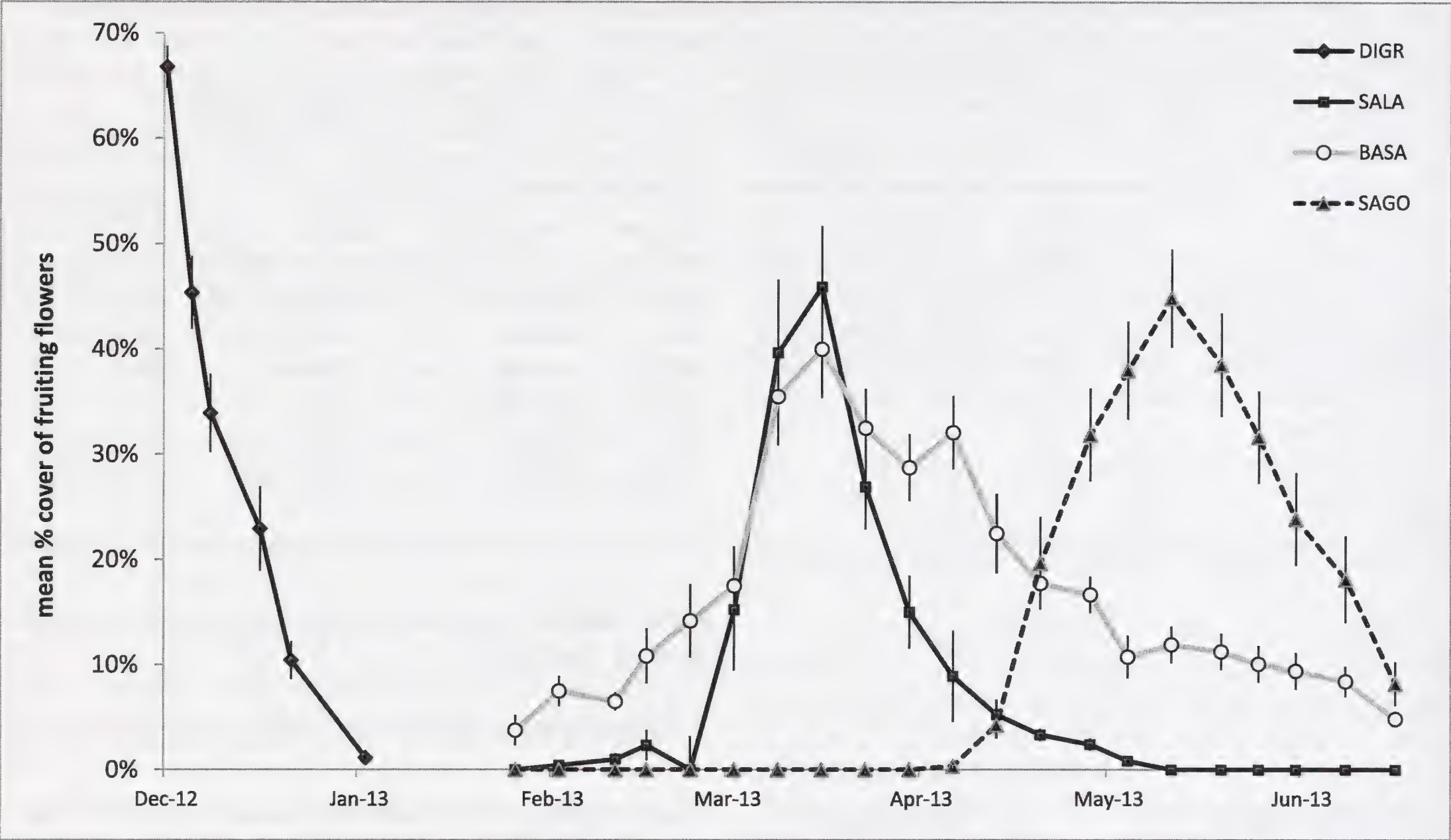


FIG. 3. Fruiting periods of the four wind-dispersed species. Data are mean percent cover (± 1 std. err.) of fruiting flowers on adult plants. DIGR = *D. graveolens*, BASA = *B. salicifolia*, SALA = *S. lasiolepis* and SAGO = *S. gooddingii*.

line, the densities of the seedlings were significantly correlated with the mean percent cover of dispersing seeds ($r = 0.638$; $P < 0.01$, $n = 140$). These results strongly suggest that seedling distributions of the four wind-dispersed species (i.e., the banding pattern) can be attributed to the timing of their seed dispersal and the simultaneous decline of the water level.

Community Development

Of the 11 species common as seedlings in the basins, only three were abundant in the older stands (Table 3). These species were *S. lasiolepis*, *S. good-*

dingii, and *B. salicifolia*, and they formed the main structural components of the older woodlands and forests in the Tijuana River Valley. *Baccharis salicifolia* dominated the moderately tall (3–5 m) woodlands surrounding the tall (8–17 m), dense riparian forests dominated by *S. lasiolepis* and *S. gooddingii*. The *S. lasiolepis*-higher and *S. gooddingii*-lower pattern, first seen in the seedlings (Fig. 2A), was still apparent in the 5 and 22 yr old forests; *S. lasiolepis* was the dominant species in the Intermediate stratum and *S. gooddingii* was the dominant species in the Low stratum in both the 5 and 22 yr old forests. Most of the other species that were abundant

TABLE 3. Percent cover values for the 11 species in riparian stands of increasing age. Data are for the High, Intermediate (Int.), and Low strata within each stand. P = present, canopy height is the maximum for the transect ($n = 3$), and canopy cover is the average for the transect ($n = 3$).

Age of stand	0.5 yr			5 yr			22 yr		
Zone	High	Int.	Low	High	Int.	Low	High	Int.	Low
Canopy height (m)	1.2	0.6	0.4	3.2	9.3	8.2	4.3	10.5	17
Canopy cover (%)	15	0	0	91	99	99	6	98	99
<i>Rumex conglomeratus</i>	69%	P							
<i>Xanthium strumarium</i>	70%		3%						
<i>Persicaria lapathifolia</i>	10%								
<i>Ricinus communis</i>		6%	16%	P	3%	44%	P	8%	P
<i>Nicotiana glauca</i>		1%	4%						
<i>Solanum americanum</i>			4%	P					
<i>Datura wrightii</i>		1%	13%						
<i>Dittrichia graveolens</i>	2%	2%							
<i>Salix lasiolepis</i>	P	1%	P	24%	100%	76%		96%	
<i>Baccharis salicifolia</i>	2%	P	P	90%	P		50%	20%	
<i>Salix gooddingii</i>		65%	P		50%	85%		12%	96%

in the basins were not present in the older woodlands, for instance *R. conglomeratus*, *X. strumarium*, *P. lapathifolia*, *N. glauca*, *Datura wrightii*, and *Dittrichia graveolens* were absent from the older woodlands.

DISCUSSION

Two Seedling Patterns and the Processes that Produced Them

Understanding patterns and the processes that produce them is a central theme in ecology (e.g., Turner et al. 2010). Here I have described two superimposed seedling distribution patterns, one formed by water-dispersed species and the other by wind-dispersed species, and I have identified the processes that produced them.

The seedling distribution pattern of water-dispersed species was straightforward; species with buoyant seeds grew high on the bank around the basin periphery, and species with sinking seeds grew in the bed. As the release of seed mimics demonstrated, river flows could sort seeds according to their buoyancy, and deposit them in different parts of the basin. Sorting of seeds based upon their buoyancy was therefore the main process that produced the seedling distribution pattern of these species.

Sorting of seeds according to their buoyancy has been shown in experimental flumes (Merritt and Wohl 2002; Chambert and James 2009), and floating seeds are thought to disperse like the 'flotation load,' while sinking seeds are carried in the water column with other non-buoyant material such as bed-load sediment and non-buoyant trash (Goodson et al. 2003; Gordon et al. 2004; Markwith and Leigh 2008; Chambert and James 2009). But sorting of seeds according to their buoyancy has rarely been examined in the field because most research on seed dispersal has been done in perennial streams, where seeds that sink typically remain in deep water and never germinate. Sinking seeds have therefore come to be considered ineffectively dispersed by flowing water (Andersson et al. 2000) or simply lost to the system (e.g., Murray 1986; Brown and Chenoweth 2008). While this may well be the case in perennial streams, this study showed that sinking seeds were effectively dispersed by flows in an intermittent system, as they germinated when the bed became exposed. Hence, non-buoyant seeds should not be overlooked in intermittent streams; the dispersal of non-buoyant seeds may be common in intermittent streams and should receive more attention in areas such as southern California, where an estimated 49% to 73% of streams are intermittent (Mazor et al. 2012).

The seedling distribution pattern of wind-dispersed species was quite different to that of water-dispersed species; wind-dispersed species grew in concentric bands on the basin's banks, each at a level on the bank that reflected the timing of their

seed production and the decline of the water level. With the gradual decline in water level during spring and summer, the moist fringe of sediment suitable for seed germination gradually moved lower on the bank, such that seeds from later-dispersing species recruited lower on the bank. The staggered timing of seed dispersal and the gradual change in the position of moist fringe were therefore the main processes that produced the seedling distribution of the wind-dispersed species. This seedling pattern was apparent because the gradually lowering pool surrounded by open sediment was ideal for seedlings to develop (Mahoney and Rood 1998). This banding pattern was also seen at three disturbed sites along the Tijuana River during 2010 (Boland 2014a). It is interesting to note that Van Splunder et al. (1995), working on the River Waal in the Netherlands, documented the sequential seed production of four Salicaceae species but found no clear patterns in the seedling distributions because water levels rose and fell several times during the seed production period, effectively mixing together the seedling distributions of the early- and later-dispersing species.

In addition to being blown through air, some wind-dispersed seeds have been shown to have a secondary mode of dispersal, which involves being pushed by the wind, or 'sailing,' on the surface of the water, termed pleustochory (Boland 2014b). Willow seeds, for example, land on a pool's surface then sail, via pleustochory, directly to their recruitment safe sites at the pool's edge. In essence, a pool can act as a collector of wind-dispersed seeds, and pleustochory serves to concentrate and deposit those seeds in their safe sites at the pool's edge. The concentration of seeds in the narrow band of moist sediment ideal for germination results in seedling densities that are orders of magnitude greater than that expected from the seed rain alone (Boland 2014b). In the current study, pleustochory concentrated and deposited both wind- and buoyant water-dispersed seeds at the pool periphery and, because it also acted on floatable debris, it helped to create the Litter Zone around the pool (Boland, personal observations).

Researchers who study dispersal typically lump buoyant water-dispersed seeds with 'buoyant' wind-dispersed seeds (Hyslop and Trowsdale 2012). It is clear, however, that the two are associated with distinctly different life histories. The water-dispersed species in this study, for example, (1) produced seeds well in advance of the winter rainy season, (2) produced seeds that could remain dormant for long periods, (3) dispersed during winter, (4) were distributed according to buoyancy characteristics of their seeds, and (5) were generally short-lived members of the community. The wind-dispersed species (1) produced seeds mainly after the rainy season, (2) produced seeds that had no dormancy and, instead, are known to have 'Very Fast Germination' (Parsons 2012; Boland 2014b; Boland unpublished data), (3) dispersed mainly during spring and summer, (4) were distributed according to seed

production period and water level decline, and (5) were generally long-lived members of the community, as three of the four species grew to become the dominants in older riparian forests. Thus, buoyant water-dispersed seeds and 'buoyant' wind-dispersed seeds represent different strategies and are best considered separately. Furthermore, it is instructive to understand that when seedlings of two species are growing together in an area, they may have arrived at different times and via different dispersal pathways.

Useful Simplifications

The Goat Canyon sediment basins were not completely natural stream reaches, but they had features that were useful for the study of seed dispersal and early community development. They were cleaned out in fall, naturally refilled with fresh sediment in winter, and left undisturbed long enough for the colonizing plant community to develop. They had no vegetation or seed bank, and had earthen bed and banks with a full range of floodwater elevations within which normal river processes were able to act. Together, these features were useful when teasing apart the superimposed seedling distribution patterns and related dispersal processes.

Ping-pong balls, as used in this study, were simple and effective seed mimics. They are normally lightweight and buoyant, but could be made to be non-buoyant and yet retain a uniform size and shape. Other researchers have used colored seeds in experimental flumes (Merritt and Wohl 2002; Chambert and James 2009) and floating wooden cubes along rivers (Nilsson et al. 1991; Andersson et al. 2000) to mimic water-dispersed seeds, and now ping pong balls can be added to the list of useful and acceptable seed mimics.

Community Development

Of the colonizing species in this study, three wind-dispersed species (*B. salicifolia*, *S. lasiolepis* and *S. gooddingii*) persist and become the dominant structural elements in early successional riparian forests in the Tijuana River Valley. Seedlings of these species quickly grow into dense thickets and then into tall, even-aged, dense stands. The banding pattern established at the time recruitment, with *S. lasiolepis*-higher and *S. gooddingii*-lower, is retained for decades (Table 3) and has been previously documented in three other clearings in the natural river (Boland 2014a). Therefore, differences in the timing of dispersal of these willows lead to both the banding pattern of their seedlings and zonation of their adults. This is one of very few examples showing a direct link between seed dispersal and the distribution of adult trees in natural habitats (Schupp and Fuentes 1995; Traveset et al. 2014). Other examples involve dispersal of seeds by monkeys (Russo 2005) and birds (Wenny 2000; Jordano and Schupp 2000).

On the other hand, the water-dispersed colonizing species do not appear to play a major role in structuring riparian communities in the Tijuana River Valley. These species tend to be herbaceous short-lived, weedy species that colonize disturbed sites and raise the local diversity but disappear from older stands as, presumably, they are outcompeted by taller-growing, longer-lived species. If water-dispersed species are the short-lived, weedy species in other riparian systems, it would explain why researchers have thus far found it so difficult to show that water-dispersal influences the long-term composition and structure of riparian communities (Andersson et al. 2000; Levine and Murrell 2003; Jansson et al. 2005).

Restoration Project Applications

Some riparian restoration sites are prepared with initial grading that removes most vegetation, topsoil and seed bank, and such sites, at least in southern California, may be somewhat similar to the Goat Canyon sedimentation basins. The results presented here show that a graded site can be colonized naturally by desirable native species and, if left undisturbed, can develop into a riparian forest with natural density, diversity and dispersion (Boland 2014a). Making use of the riparian habitat's considerable capacity for natural recovery is called 'natural restoration' or 'passive revegetation' (Faber et al. 1989; Briggs 1996; Sher et al. 2002; Boland 2014a). To be most successful, a natural restoration project should aim to maximize recruitment of the wind-dispersed species that become the dominant riparian forest trees, and to do so by ensuring that the water's edge sweeps across the restoration site during the seed dispersal period of those species (March to June in southern California). This type of natural restoration is likely to be particularly effective at sites that are cleared beforehand, have abundant seed sources nearby, include a pool with a declining water level, and are left undisturbed after the seedlings colonize (Briggs 1996). The results of this study suggest that knowing the mode and timing of seed dispersal will allow for a more accurate prediction of natural recruitment and will therefore be extremely helpful in the natural revegetation of restored riparian areas.

ACKNOWLEDGMENTS

I thank Deborah Woodward for helpful discussions and comments on early drafts of this manuscript, California State Parks for making the Goat Canyon area available for study, and two anonymous reviewers for thoughtful reviews that greatly improved the manuscript.

LITERATURE CITED

- ANDERSSON E., C. NILSSON, AND M.W. JOHANSSON. 2000. Plant Dispersal in Boreal Rivers and its Relation to the Diversity of Riparian Flora. *Journal of Biogeography* 27: 1095–1106.

- BALDWIN, B. G., D. H. GOLDMAN, D. J. KEIL, R. PATTERSON, T. J. ROSATTI, AND D. H. WILKEN. (eds.). 2012. The Jepson Manual: vascular plants of California. University of California Press, Berkeley, CA.
- BOLAND, J. M. 2014a. Factors determining the establishment of plant zonation in a southern Californian riparian woodland. *Madroño* 61:48–63.
- . 2014b. Secondary dispersal of willow seeds: sailing on water into safe sites. *Madroño* 61:388–398.
- BRIGGS, M. K. 1996. Riparian ecosystem recovery in arid lands. University of Arizona Press, Tucson, AZ.
- BROWN, R. L. AND J. CHENOWETH. 2008. The effect of Glines Canyon Dam on hydrochorous seed dispersal in the Elwha River. *Northwest Science* 82:197–209.
- BULLOCK, J. M. AND R. T. CLARKE. 2000. Long distance seed dispersal by wind: measuring and modeling the tail of the curve. *Oecologia* 124:506–521.
- CHAMBERT, S. AND C. S. JAMES. 2009. Sorting of seeds by hydrochory. *River Research and Applications* 25:48–61.
- DANVIND, M. AND C. NILSSON. 1997. Seed floating ability and distribution of alpine plants along a northern Swedish river. *Journal of Vegetation Science* 8:271–276.
- FABER, P. A., E. KELLER, A. SANDS, AND B. M. MASSEY. 1989. The ecology of riparian habitats of the southern California coastal region: a community profile. United States Department of the Interior, Fish and Wildlife Service, National Wetlands Research Center, Biological Report 85 (7.27).
- GOODSON, J. M., A. M. GURNELL, P. G. ANGOLD, AND I. P. MORRISSEY. 2003. Evidence for hydrochory and the deposition of viable seeds within winter flow-deposited sediments: the River Dove, Derbyshire, UK. *River Research and Applications* 19:317–334.
- GORDON, N. D., T. A. MCMAHON, B. L. FINLAYSON, C. J. GIPPEL, AND R. J. NATHAN. 2004. Stream hydrology: an introduction for ecologists. Wiley, Chichester, UK.
- GURNELL, A. M., A. J. BOITSIDIS, K. THOMPSON, AND N. J. CLIFFORD. 2006. Seed bank, seed dispersal and vegetation cover: colonization along a newly created river channel. *Journal of Vegetation Science* 17:665–674.
- GURNELL A., T. THOMPSON, J. GOODSON, AND H. MOGGRIDGE. 2008. Propagule deposition along river margins: linking hydrology and ecology. *Journal of Ecology* 96:553–565.
- HYSLOP, J. AND S. TROWSDALE. 2012. A review of hydrochory (seed dispersal by water) with implications for riparian rehabilitation. *Journal of Hydrology* 51:137–152.
- JANSSON R., U. ZINKO, D. M. MERRITT, AND C. NILSSON. 2005. Hydrochory increases riparian plant species richness: a comparison between a free flowing and a regulated river. *Journal of Ecology* 93:1094–1103.
- JOHANSSON, M. E., C. NILSSON, AND E. NILSSON. 1996. Do rivers function as corridors for plant dispersal? *Journal of Vegetation Science* 7:593–598.
- JORDANO, P. AND E. W. SCHUPP. 2000. Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs* 70:591–615.
- KARRENBERG, S., P. J. EDWARDS, AND J. KOLLMANN. 2002. The life history of Salicaceae living in the active zone of floodplains. *Freshwater Biology* 47:733–748.
- LEVINE, J. M. AND D. MURRELL. 2003. Community-level consequences of seed dispersal patterns. *Annual Review of Ecology and Systematics* 34:549–574.
- LIGHTNER, J. 2011. San Diego County native plants. San Diego Flora, San Diego, CA.
- MAHONEY, J. M. AND S. B. ROOD. 1998. Streamflow requirements for cottonwood seedling recruitment—an integrative model. *Wetlands* 18:634–645.
- MARKWITH, S. H. AND D. S. LEIGH. 2008. Subaqueous hydrochory: open-channel hydraulic modeling of non-buoyant seed movement. *Freshwater Biology* 53:2274–2286.
- MATLACK, G. R. 1987. Diaspore size, shape, and fall behavior in wind-dispersed plant species. *American Journal of Botany* 74:1150–1160.
- MAZOR, R., K. SCHIFF, P. ODE, AND E. D. STEIN. 2012. Final Report on Bioassessment in Nonperennial Streams. Report to the State Water Resources Control Board. Technical Report 695:1–37.
- MERRITT, D. M. AND E. E. WOHL. 2002. Processes governing hydrochory along rivers: hydraulics, hydrology, and dispersal phenology. *Ecological Applications* 12:1071–1087.
- MURRAY, D. 1986. Seed Dispersal. Academic Press, CA.
- NATHAN R., G. G. KATUL, H. S. HORN, S. M. THOMAS, R. OREN, R. AVISSAR, S. W. PACALA, AND S. A. LEVIN. 2002. Mechanisms of long-distance dispersal of seeds by wind. *Nature* 418:409–413.
- NATHAN, R. AND H. C. MULLER-LANDAU. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* 15:278–285.
- NILSSON, C., R. L. BROWN, R. JANSSON, AND D. M. MERRITT. 2010. The role of hydrochory in structuring riparian and wetland vegetation. *Biological Reviews* 85:837–858.
- NILSSON, C., M. GARDFJELL, AND G. GRELSSON. 1991. Importance of hydrochory in structuring plant communities along rivers. *Canadian Journal of Botany* 69:2631–2633.
- PARSONS, R. F. 2012. Incidence and ecology of very fast germination. *Seed Science Research* 22:161–167.
- RUSSO, S. E. 2005. Linking seed fate to natural dispersal patterns: factors affecting predation and scatter-hoarding of *Virola calophylla* seeds in Peru. *Journal of Tropical Ecology* 21:243–253.
- SCHUPP, E. W. AND M. FUENTES. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. *Ecoscience* 2:267–275.
- SHER, A. A., D. L. MARSHALL, AND J. P. TAYLOR. 2002. Establishment patterns of native *Populus* and *Salix* in the presence of invasive nonnative *Tamarix*. *Ecological Applications* 12:760–772.
- SOKAL, R. R. AND F. J. ROHLF. 1995. Biometry. W.H. Freeman and Company, New York, NY.
- TABACCHI, E., A.-M. PLANTY-TABACCHI, L. ROQUES, AND E. NADAL. 2005. Seed inputs in riparian zones: implications for plant invasion. *River Research and Applications* 21:299–313.
- TRAVESET, A., R. HELENO, M. NOGALES, AND R. S. GALLAGHER. 2013. The ecology of seed dispersal. Pp. 62–93 in R.S. Gallagher (ed.) *Seeds: the ecology of regeneration in plant communities*. CAB International, Boston, MA.
- TURNER, M. G., R. H. GARDNER, AND R. V. O'NEILL. 2010. Landscape Ecology in Theory and Practice: Pattern and Process. Springer-Verlag, New York, NY.
- VAN SPLUNDER I., H. COOPS, L. VOESENEK, AND C. BLOM. 1995. Establishment of alluvial forest species in floodplains: the role of dispersal timing, germination

- characteristics and water level fluctuations. *Acta Botanica Neerlandica* 44:269–278.
- VOGT, K., L. RASRAN, AND K. JENSEN. 2006. Seed deposition in drift lines during an extreme flooding event—Evidence for hydrochorous dispersal? *Basic and Applied Ecology* 7:422–432.
- . 2007. Seed deposition in drift lines: opportunity or hazard for species establishment? *Aquatic Botany* 86:385–392.
- WENNY, D. G. 2000. Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. *Ecological Monographs* 70:331–351.
- WILLSON, M. F. 1983. *Plant reproductive ecology*. John Wiley and Sons, New York, NY.
- WILLSON, M. F. AND A. TRAVESET. 2000. The ecology of seed dispersal. Pp. 85–110 *in* M. Fenner (ed.) *Seeds: the ecology of regeneration in plant communities*. CAB International, Boston, MA.